Geographic variation in Socotra Sparrows *Passer insularis*

by Peter G. Ryan, Lisa Nupen, Barrie Rose & Ahmed Saeed Suleiman

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SUMMARY.—Socotra Sparrow *Passer insularis* is the only Socotran endemic landbird that occurs on the other islands of the Socotra archipelago. It is widely reported to occur on Abd 'Al Kuri, but the populations on Samha and Darsa were unknown until very recently. We present genetic data to support a recent call to elevate the Abd 'Al Kuri population to species level, Abd 'Al Kuri Sparrow *P. hemileucus*. Sequence divergence in two mitochondrial genes between *hemileucus* and *insularis* is 1.3–1.7%. The evolutionary history of the sparrows on Socotra cannot be inferred reliably until other taxa in the *P. motitensis* superspecies have been sampled. Sparrows on Samha are not genetically distinct from those on the main island of Socotra, but are appreciably smaller and should be recognised subspecifically. Birds on nearby Darsa were not caught, but photographs suggest they are similar to those on Samha. The Abd 'Al Kuri Sparrow qualifies as Vulnerable, due to its small population (<1,000 mature birds) and limited range (<100 km^2).

The Socotra archipelago off the Horn of Africa consists of Socotra, a large continental island, and several smaller islands. The main island of Socotra is an Endemic Bird Area with at least six endemic landbird species (Stattersfield *et al.* 1998, Kirwan & Grieve 2007). Of these species, only the Socotra Sparrow *Passer* [*motitensis*] *insularis* occurs on other islands in the archipelago: Abd 'Al Kuri, Samha and Darsa (Fig. 1). Until recently, little had been published about geographic variation in sparrows at Socotra. Birds collected on Abd 'Al Kuri, the largest of the satellites, were described as *Passer hemileucus* (Ogilvie-Grant & Forbes 1899), but this has been ignored by most recent authors, who failed to recognise the Abd 'Al Kuri population even as a subspecies (see Kirwan 2008 for a review).

Kirwan (2008) re-examined specimens of the sparrow from Abd 'Al Kuri, and argued that it warrants species status, based on the paler plumage and smaller size. However, he did not consider any genetic markers, nor was he able to assess the status of sparrows on

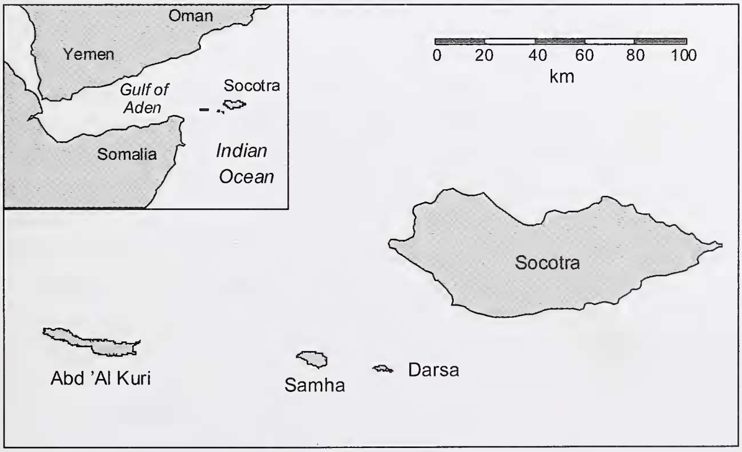

Figure 1. The Socotra archipelago, showing the four main islands and their position relative to the Horn of Africa and the Arabian Peninsula.

the other two islands in the group, Samha and Darsa, where sparrows were not known to occur until recently (Kirwan 2008). In this paper we confirm that Abd 'Al Kuri Sparrows are genetically distinct from those on Socotra, and demonstrate that the sparrows on Samha are appreciably smaller than other Socotra Sparrows. We also suggest that the Abd 'Al Kuri Sparrow qualifies as Vulnerable, due to its small population (<1,000 mature birds) and limited range (<100 km^2).

Materials and Methods

PGR and BR visited Socotra in March–April 2007 as part of a survey of the outer islands (Fig. 1) led by ASS under the aegis of the Socotra Conservation & Development Programme. We spent a week on the main island, two days on Abd 'Al Kuri, two days on Samha and a few hours on Darsa. Sparrows were caught in mist-nets on the northern coastal plain of Socotra (12°36′N, 53°42′E) on 25 March and 4 April, and at a small spring behind the settlement at the west end of Samha (12°10′N, 53°01′E) on 1 April. It was too windy and exposed to catch sparrows using mist-nets in the conventional way on Abd 'Al Kuri, but we managed to trap four individuals by dropping a net over birds feeding on rice at the main settlement (12°11′N, 52°14′E) on 29 March. Only a few sparrows were seen on Darsa. None was trapped during our brief visit ashore on 2 April, but a breeding pair was photographed. Photographs were taken of birds at other locations too, permitting comparison of plumage features identified by Kirwan (2008).

Sparrows caught were measured: flattened wing-chord to the nearest 1 mm, and tarsus, total head, culmen, and bill depth to the nearest 0.1 mm. Juveniles could not be sexed reliably, but other birds were sexed on the basis of plumage characters (see Kirwan 2008). Additional measurements (wing length, tail length, bill length to skull and bill depth) of specimens from Socotra and Abd 'Al Kuri were supplied by G. M. Kirwan (*in litt*. 2007); his measuring protocols are described in Kirwan (2008). A small amount of blood was collected from the brachial vein of a subset of birds and stored in ethanol.

DNA was extracted from this blood with a DNeasy tissue kit (Qiagen) using the animal tissue protocol. Two mitochondrial (mt) DNA target regions were amplified: partial cytochrome-*b* (cyt-*b*, 273 bp) and partial NADH dehydrogenase subunit 3 (ND3, 320 bp) fragments. The primer sequences used for cyt-*b* were GGATTCTCAGTAGACAACCC (523F, forward, Thomassen *et al*. 2003) and GTAGGATGGCGTAGGCGA (827R, reverse, van der Meij *et al*. 2005) and those used for ND3 were GACTTCCAATCTTTAAAATCTGG (L10775, forward, Chesser 1999) and GATTTGTTGAGCCGAAATCAAC (H11151, reverse, Chesser 1999).

PCRs were carried out on a GeneAmp PCR System 2700 (Applied Biosystems) and comprised an initial denaturation step at 94°C for three minutes, followed by 35 cycles of 94°C for 60 seconds (denaturation), 54°C for 30 seconds (primer annealing) and 72°C for 60 seconds (extension), with a final extension step of 72°C for five minutes. Bands were cut out and gel purified using the Promega Wizard PCR Clean-up Kit (Promega, UK). Cycle sequencing was carried out with the ABI PRISM Big Dye Terminator V3.1 cycle sequencing Ready Reaction Kit (Applied Biosystems). Sequencing was undertaking using BigDye Technology on an ABI PRISM 3100 Genetic Analyser (Applied Biosystems).

Sequences were inspected in BioEdit (Hall 1999) and checked using FinchTV (Geospiza Inc. v. 1.4.0). Any sequence with ambiguous bases or missing data was discarded. Sequences were aligned and edited with BioEdit Sequence Alignment Editor v. 7.0.4.1 (Hall 1999), which includes Clustal W for multiple sequence alignments (Thompson *et al*. 1997). Unique haplotypes were identified and sequence variation between populations was estimated using DnaSP (Rozas *et al*. 2003).

Unweighted Parsimony (MP), maximum likelihood (ML) and Bayesian approaches were used to infer phylogeny from sequence data for each gene region separately and for the combined sequence data. Parsimony-based analyses were conducted in PAUP* 4.0b10 (Swofford 2002), using branch and bound and heuristic searches, tree-bisection-reconnection (TBR) branch swapping, and 1,000 bootstrap replicates to assess nodal support (Felsenstein 1985). Maximum likelihood analyses were conducted using PhyML (Guindon & Gascuel 2003) using a full heuristic search with 1,000 random addition replicates and TBR branch-swapping.

Bayesian inference was implemented in MrBayes v3.1.2, using a mixed model (GTR+I+G for each target region). Markov Chain Monte Carlo (MCMC) analyses (chain length = 10 million, trees sampled every 1,000 generations, burn-in set at 10% [1,000 trees] for all MCMC analyses) were repeated four times. MCMC convergence was determined by the standard deviation of split frequencies approaching zero and the PSRF (potential scale reduction factor) reaching 1.0 for all parameters.

Sequence data for outgroup *Passer* spp. were obtained from GenBank. The outgroups used were Cape Sparrow *P. melanurus* (GenBank accession numbers (L77905, AY329468.1), Russet Sparrow *P. rutilans* (AF230912.1), House Sparrow *P. domesticus* (AY030163.1), Eurasian Tree Sparrow *P. montanus* (AY030164.1, EF102488.1, AB159160.1), Saxaul Sparrow *P. ammodendri* (AF230915.1) and Sudan Golden Sparrow *P. luteus* (AF230919). Sequences obtained in this study were deposited with GenBank (accession numbers EU478411–22 for ND3 and EU478423–34 for cyt-*b*).

Results

Twenty sparrows were caught on Socotra, 15 on Samha and four on Abd 'Al Kuri. Restricting the analysis to birds from Socotra, there was no significant difference in mean wing length or bill depth measurements from live birds and those from museum skins (t_{53}=0.20, 0.57, *P*>0.8, 0.5, respectively). A biplot of these characters for the pooled samples revealed very little overlap between populations from each island, with the greatest difference between birds from Socotra and Samha (Fig. 2). Comparison of birds caught on Socotra and Samha during this study confirms the markedly smaller size of birds on Samha in all dimensions (Table 1). Within island populations, males averaged slightly larger than females, but these differences were smaller than the differences between islands. Socotra birds averaged 8–12% larger in all dimensions except bill depth, which was 26% greater for both sexes combined.

Sparrows on Samha resembled Socotra Sparrows more closely than Abd 'Al Kuri Sparrows, they having darker, more saturated plumage (Table 2, Figs. 3–6). Females from Samha and Socotra were quite similar, but Samha males differed from those on Socotra in having small black bibs largely confined to the chin and throat, not extending onto the breast, and in having more extensive whitish tips to the median wing-coverts. They also had less extensive black on the ear-coverts than most Socotra Sparrows, although this feature is variable on Socotra. The birds photographed on Darsa resembled birds from Samha.

Partial cyt-*b* sequences (273 bp) were obtained from 12 sparrows (four from Socotra, five from Samha and three from Abd 'Al Kuri), and partial ND3 sequences (320 bp) from four sparrows from each island. Two haplotypes, differing by three transitions, were found in the partial cyt-*b* sequences, one confined to Abd 'Al Kuri and the other to Socotra and Samha (Table 4). Sequences of ND3 were more variable, with five haplotypes found: four on Socotra, of which one was also found in all birds from Samha, and another haplotype on Abd 'Al Kuri (Table 4). The difference between the Abd 'Al Kuri haplotype and the closest Socotra / Samha haplotype was four transitions. Mean sequence divergence among island

TABLE 1

Mensural differences between Socotra Sparrows *Passer insularis* on Samha and the main island of Socotra (mean ± SD and range; all measurements in mm; excludes juveniles). Significance tested with Mann-Whitney U-tests.

	Socotra	Samha	Significance
Males	*n*=9	*n*=5	
Wing	75.2±1.8 (73–78)	70.2±0.5 (70–71)	U=45, *P*<0.001
Tarsus	21.2±0.5 (20.4–22.2)	19.4±0.2 (19.2–19.8)	U=45, *P*<0.001
Total head	34.5±0.4 (33.9–35.4)	31.5±0.4 (31.1–32.1)	U=45, *P*<0.001
Culmen	14.4±0.5 (13.7–15.1)	13.0±0.4 (12.6–13.6)	U=45, *P*<0.001
Bill depth	9.4±0.2 (9.2–9.7)	7.6±0.1 (7.4–7.7)	U=45, *P*<0.001
Females	*n*=9	*n*=9	
Wing	74.8±1.5 (72–77)	68.4±1.0 (67–70)	U=81, *P*<0.001
Tarsus	21.2±0.7 (20.0–21.8)	19.0±0.3 (18.4–19.4)	U=81, *P*<0.001
Total head	35.2±0.8 (34.0–36.3)	31.7±0.4 (31.2–32.2)	U=81, *P*<0.001
Culmen	14.9±0.6 (14.2–16.2)	13.2±0.3 (12.8–13.6)	U=81, *P*<0.001
Bill depth	9.4±0.2 (9.1–9.7)	7.4±0.1 (7.3–7.5)	U=81, *P*<0.001

TABLE 2

Plumage differences among male sparrows in the Socotra archipelago.

Character	Socotra	Samha	Abd 'Al Kuri
Head-sides	rich chestnut	rich chestnut	sandy rufous
Wing-coverts	rich chestnut	rich chestnut	sandy rufous
Underparts	pale grey	pale grey	sandy buff
Back and rump	grey	grey	sandy grey
Mantle streaking	heavy	moderate	moderate–light
Black on ear-coverts	extensive*	limited	limited
Bib	extends onto breast*	confined to throat	confined to throat

*Some variation; one male on Socotra had a rather narrow black line on its ear-coverts and the bib barely extending onto the breast

populations was limited between Socotra and Samha, but was 1.3–1.7% between these islands and Abd 'Al Kuri (Table 3).

In all phylogenetic analyses of the genetic sequence data (cyt-*b*, ND3 and the combined dataset), birds from the three island populations formed a monophyletic group, with Socotra and Samha clustered together, distinct from birds on Abd 'Al Kuri (Fig. 7). The Abd 'Al Kuri clade had consistently high nodal support (>90% for each gene region separately and for the combined dataset). There was little consistency in the identification of a closest relative among other sparrows for which sequence data are available in GenBank. However, no sequences were available for other members of the *Passer motitensis* superspecies.

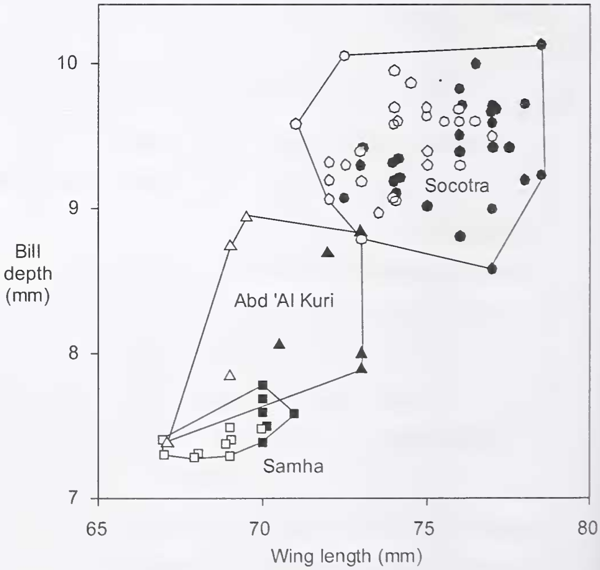

Figure 2. Biplot of wing length versus bill depth in three island populations of Socotra sparrows, based on specimens (G. M. Kirwan *in litt*. 2007) and live birds. Open symbols are females, solid symbols males.

TABLE 3
Genetic divergence (%) between island populations of Socotra sparrows.
Cyt-*b* top right above diagonal, ND3 lower left below diagonal.

Locality	Socotra	Samha	Abd 'Al Kuri
Socotra	–	0.0	1.48
Samha	0.40	–	1.48
Abd 'Al Kuri	1.66	1.26	—

TABLE 4
Haplotype frequencies for island populations of Socotra sparrows.

Locality	Socotra	Samha	Abd 'Al Kuri
ND3 Haplotype 1	0	0	4
ND3 Haplotype 2	1	4	0
ND3 Haplotype 3	1	0	0
ND3 Haplotype 4	1	0	0
ND3 Haplotype 5	1	0	0
Cyt-*b* Haplotype 1	0	0	3
Cyt-*b* Haplotype 2	4	5	0

Discussion

Our findings support Kirwan's (2008) call to recognise Abd 'Al Kuri Sparrow *Passer hemileucus* as a species, because it is diagnosably distinct in its plumage and morphology, and shows significant molecular divergence from Socotra Sparrows. Based on a rate of change in cyt-*b* of 2% per one million years (Lovette 2004), sparrows on Abd 'Al Kuri have been isolated from those on Socotra and Samha for around 0.8 million years. However, recent studies have found that substitution rates at the avian cyt-*b* gene vary considerably across lineages, and can be appreciably slower than 2% per million years (Pereira & Baker 2006). Allende *et al.* (2001) estimated a rate of roughly 0.4% per million years for *Passer*, suggesting that sparrows on Abd 'Al-Kuri diverged from those on Socotra / Samha some 3.5 million years ago. We attempted to date this divergence by implementing a relaxed molecular clock (Drummond *et al.* 2006), but without fossil evidence to calibrate the clock, we were unable to obtain acceptable levels of confidence around the nodes of interest. Attempts at constraining the root of the tree using an approximate time for the appearance of the genus *Passer* or geological constraints such as the time of the split of Socotra from mainland Africa proved ineffective at improving confidence (highest posterior density regions). In the absence of sequence data from other taxa in the *motitensis* superspecies, we cannot test whether the two species arose as a result of dispersal / vicariance within the archipelago, or from separate colonisation events, presumably from the Horn of Africa.

The apparent lack of gene flow between birds on Abd 'Al Kuri and the rest of the archipelago is consistent with the greater isolation of Abd 'Al Kuri. It is 63 km from Samha and 105 km from Socotra, whereas Samha and Darsa are only 17 km apart, and 46 and 36 km from Socotra, respectively. Indeed, Abd 'Al Kuri is closer to the African mainland (96 km) than it is to Socotra. Abd 'Al Kuri also has been isolated from the rest of the archipelago for longer than have Samha and Darsa. Socotra split from Africa and Arabia as a result of block faulting during the Tertiary period, probably in association with the formation of the Gulf of Aden some 36MYA (Miller & Morris 2004, Cheung *et al.* 2006). Samha and Darsa formed through erosion of the original Socotra massif; they are separated from the main island by waters <50 m deep, whereas Abd 'Al Kuri is separated from the other islands by a channel >200 m deep (Klaus & Turner 2004). Abd 'Al Kuri exhibits a greater level of species

Figure 3. Typical male Socotra Sparrow *Passer insularis*, lowlands of Socotra, late March 2007 (P. G. Ryan)

Figure 4. Typical male Socotra Sparrow *Passer insularis*, Samha, late March 2007 (P. G. Ryan)

Figure 5. Male Socotra Sparrow *Passer insularis*, Darsa, early April 2007 (B. Rose)

Figure 6. Typical male Abd 'Al Kuri Sparrow *Passer hemileucus*, Abd 'Al Kuri, late March 2007 (P. G. Ryan)

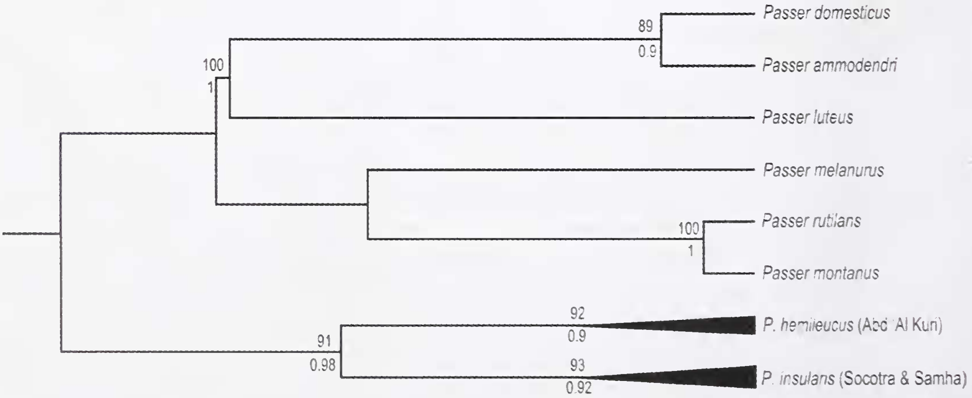

Figure 7. Unrooted phylogeny of Socotra sparrows based on the combined partial cytochrome-*b* and NADH subunit 3 sequence data. Values given for nodes are Bayesian posterior probabilities (below node) and maximum parsimony bootstrap support (above node).

endemism among other terrestrial vertebrates (e.g., reptiles, Rösler & Wranik 2004) as well as flowering plants (Miller & Morris 2004), compared to Samha and Darsa.

Despite the limited genetic distance between sparrow populations on Socotra and Samha, the birds on Samha are appreciably smaller, with no overlap in any of the measurements among birds of the same sex (Table 1). Males also differ in several plumage characters (Table 2). The Samha population probably warrants recognition as a distinct taxon, but its formal naming awaits collection of a specimen.

The paucity of genetic diversity within populations on Samha and Abd 'Al Kuri is consistent with the much smaller populations on these islands. Socotra is a large island (3,625 km^2), and the sparrow is the most abundant of the endemic landbirds, with an estimated population in excess of 200,000 birds (Kirwan 2008). There are many fewer sparrows on the other islands, in part due to their smaller size but also their much drier climate, linked to their lower elevation (Miller & Morris 2004, Cheung *et al.* 2006). Abd 'Al Kuri (133 km^2) is the second-largest of the archipelago, but is very hot and dry, with little vegetation over much of the island, and no surface water (Ripley & Bond 1966). Sparrows were fairly common at the main settlement, Khisat Salha, where perhaps 100 scavenged among refuse. At dusk, pairs of adults were observed leaving the settlement along dry drainage lines with scattered shrubs, apparently to roost in taller vegetation in the foothills of the high limestone mountain range that runs along the spine of the island east of Khisat Salha. Several pairs were also found in the better-vegetated wadis running down from these mountains well away from the village. There appears to be little other suitable habitat on the island. During a circumnavigation by small boat the only area we saw with sufficient vegetation to support sparrows was the main mountain chain. Sparrows were absent from the village near the main landing site on the north coast, but ASS has recorded them previously around a small fishing camp at the extreme western end. We estimate a total population of <1,000 mature individuals. The Abd 'Al Kuri Sparrow qualifies as Vulnerable (BirdLife International 2004), due to its small population (criterion D1) and limited range (D2).

Samha (41 km^2) is even smaller than Abd 'Al Kuri, but the island is dominated by a high limestone mountain range that runs virtually the length of the island, with springs at its eastern and western ends. Sparrows were abundant around these springs and at the settlement at the western end. The total population almost certainly is greater than that on Abd 'Al Kuri, but probably <5,000 birds. Darsa is the smallest island (16 km^2) and is uninhabited. Like Samha, it has a limestone mountain running the length of the island. We observed a few sparrows along the southern sea cliffs during a circumnavigation by small boat, and found a pair nesting in a cavity in the roof of a cave on the northern shore. The total population probably is <1,000 birds.

Given considerable interest in the evolution of island birds, it is remarkable that the diversity of sparrows at the Socotra archipelago has been largely ignored (Kirwan 2008). Further studies are required to assess whether the smaller size of sparrows on the outer islands are adaptive (e.g. related to dietary differences or different physiological constraints), or merely a consequence of founder effects and subsequent drift.

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Addresses: Peter G. Ryan, Lisa Nupen & Barrie Rose, Percy FitzPatrick Institute, DST / NRF Centre of Excellence, University of Cape Town, Rondebosch 7701, South Africa, e-mail: peter.ryan@uct.ac.za. Ahmed Saeed Suleiman, Socotra Conservation & Development Programme, Ministry of Water & Environment, P.O. Box 16494, Sana'a, Yemen.